PRELIMINARY REPORT ON THE MIOCENE VERTEBRATES FROM ARRISDRIFT, SOUTH WEST AFRICA

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(With 13 figures and 11 tables)

ABSTRACT

At least 28 vertebrate species, of which 22 are mammals, are recorded from the early middle Miocene (*c.* 16 m.y. old) fossil occurrence at Arrisdrift on the Orange River in South West Africa. The material postdates Miocene vertebrates previously recorded from the Namib desert. The mammals include at least 3 new species (a hyracoid, a palaeomerycid and an ochotonid), while there are at least 8 genera represented which have not hitherto been known in southern Africa. *Austrolagomys simpsoni* Hopwood, 1929, is referred to *Kenyalagomys* Whitworth, 1954, and *Prohyrax* is placed in the Pliohyracinae, a group which apparently had its origins in southern Africa.

CONTENTS

INTRODUCTION

Until recently the only substantial information on southern African Miocene terrestrial vertebrates came from several small fossil assemblages collected in the southern Namib desert (Stromer 1926; Hopwood 1929; Hamilton & Van Couvering 1977). The described material is limited in both quality and quantity. The discovery of a new Miocene vertebrate locality in terrace deposits at Arrisdrift on the Orange River further south in the same region (Fig. 1) has proved an important addition to the local Miocene fossil record (*South African Journal of Science* 1976; Corvinus & Hendey 1978). The number of fossils already collected at Arrisdrift exceeds the combined total from the other Namib desert occurrences, although the quality of the specimens is not necessarily superior. The presence on the subcontinent of several taxa has been revealed for the first time. These include the deinothere, *Prodeinotherium hobleyi* (Harris 1977).

The fossils were discovered in a prospect pit (Pit 2 of Drill-line AD 8) in deposits being investigated by the Consolidated Diamond Mines of South

1

West Africa (Pty) Ltd. Further fossiliferous deposit has since been exposed by extending the original pit, but the limits of the occurrence have not been established.

The material already prepared includes remains of at least 28 vertebrate species, of which 22 are mammals (Table 1). Most have yet to be positively identified and studies have so far been confined largely to cranial material, which is much less common than postcranial bones. The condition of specimens varies considerably, some being well preserved and reasonably complete, but most having suffered post-mortem damage. The fossils occur in a poorly sorted

TABLE 1

The vertebrates from Pit 2/AD 8 at Arrisdrift, South West Africa.

OSTEICHTHYES	. . . .	gen. et sp(p). indet.
AMPHIBIA	. . . .	gen. et sp. indet.
REPTILIA		
Squamata	. . . .	gen. et sp. indet.
Crocodilia	. . . .	*? Crocodylus niloticus*
Chelonia .	. . . .	gen. et sp(p). indet.
AVES	. . . .	gen. et spp. indet.
MAMMALIA		
Insectivora		
Macroscelididae	. . . . . .	*Myohyrax* cf. *oswaldi*
Carnivora		
Amphicyonidae	. . . . . .	*Amphicyon* cf. *steinheimensis*
Amphicyonidae or Ursidae .	. . . .	gen. et sp. indet.
?Ursidae .	. . . .	?Hemicyoninae gen. & sp. indet.
?Felidae .	. . . .	*? Metailurus* sp.
Mustelidae	. . . .	*? Ischyrictis* sp.
indet.	. . . .	gen. & sp. indet.
Hyracoidea		
Procaviidae	. . . .	*Prohyrax* n. sp.
Proboscidea		
Gomphotheriidae .	. . . . . .	gen. et sp. indet.
Deinotheriidae	. . . .	*Prodeinotherium hobleyi*
Perissodactyla		
Rhinocerotidae	. . . . . .	*Dicerorhinus* sp.
Artiodactyla		
Suidae	. . . .	gen. et sp. indet.
		Lopholistriodon moruoroti
Tragulidae	. . . .	*Dorcatherium* cf. *pigotti*
Palaeomerycidae	. . . . . .	*Climacoceras* sp. nov.
Bovidae .	. . . .	gen. et sp. indet.
Pecora	. . . .	gen. et sp. indet.
Lagomorpha		
Ochotonidae .	. . . . . .	*Kenyalagomys* sp. nov.
Rodentia		
?Bathyergidae	. . . . . .	*? Bathyergoides* sp.
Thryonomyidae	. . . . . .	*Paraphiomys pigotti*
indet.	. . . .	gen. et spp. indet.

fluvial gravel and their imperfections are due mainly to their having been transported by water in a high-energy environment. Only one instance is recorded of skeletal elements occurring in articulation and, in addition to disarticulation and fragmentation, many specimens are abraded and distorted. Incrustations of gypsum have etched and even destroyed parts of some specimens. Since the deposit incorporating the fossils is consolidated, power tools were required during their excavation and this has caused further damage to specimens. In spite of its shortcomings, the Arrisdrift fossil assemblage is perhaps the most important one of Miocene age yet discovered in southern Africa.

The purpose of the present report is to place on record some details of the nature and number of specimens belonging to the various taxa already recognized. With the exception of the deinothere teeth, none of the material has been thoroughly studied, although such studies will be undertaken by various authorities in the future. The geological investigation of the deposits in the vicinity of Arrisdrift is being undertaken by employees of the mining company prospecting the area.

The specimens discussed in this report are housed in the Department of Cenozoic Palaeontology at the South African Museum, Cape Town. The full catalogue numbers begin SAM–PQ–, which identify the institution and department concerned, but this lettering is omitted in the text and only the site prefix (AD) and serial numbers of individual specimens are given. The full site reference is Arrisdrift, Pit 2/AD 8.

OTHER MIOCENE VERTEBRATE OCCURRENCES IN THE NAMIB DESERT

The first Miocene vertebrates from the southern Namib desert were discovered during the First World War and were described in a series of papers by Stromer (1922, 1923, 1924, 1926). This material came from three localities, namely, Elisabethfeld, 38 km south of Lüderitz; a borehole near Plant 4 of the Kolonial Bergbau Gesellschaft, 20 km south of Lüderitz (= Elisabeth Bay Pan, see Greenman 1966); and Langental near Bogenfels, 80 km south of Lüderitz (Fig. 1).

Subsequently Hopwood (1929) described another small assemblage of specimens from the same region, but his material lacks precise locality data and was recorded as being from 'south of Lüderitz Bay'.

Little additional material was collected in the region in the decades which followed. The South African Museum has an undescribed ruminant mandible fragment (SAM–PQ–G 8356) from Bogenfels, which may be a synonym of Stromer's Langental locality. Some fragmentary material was collected by Greenman (1966) from Fiskus and Grillental in the Elisabethfeld area. This material is also in the South African Museum, but includes little that is diagnostic.
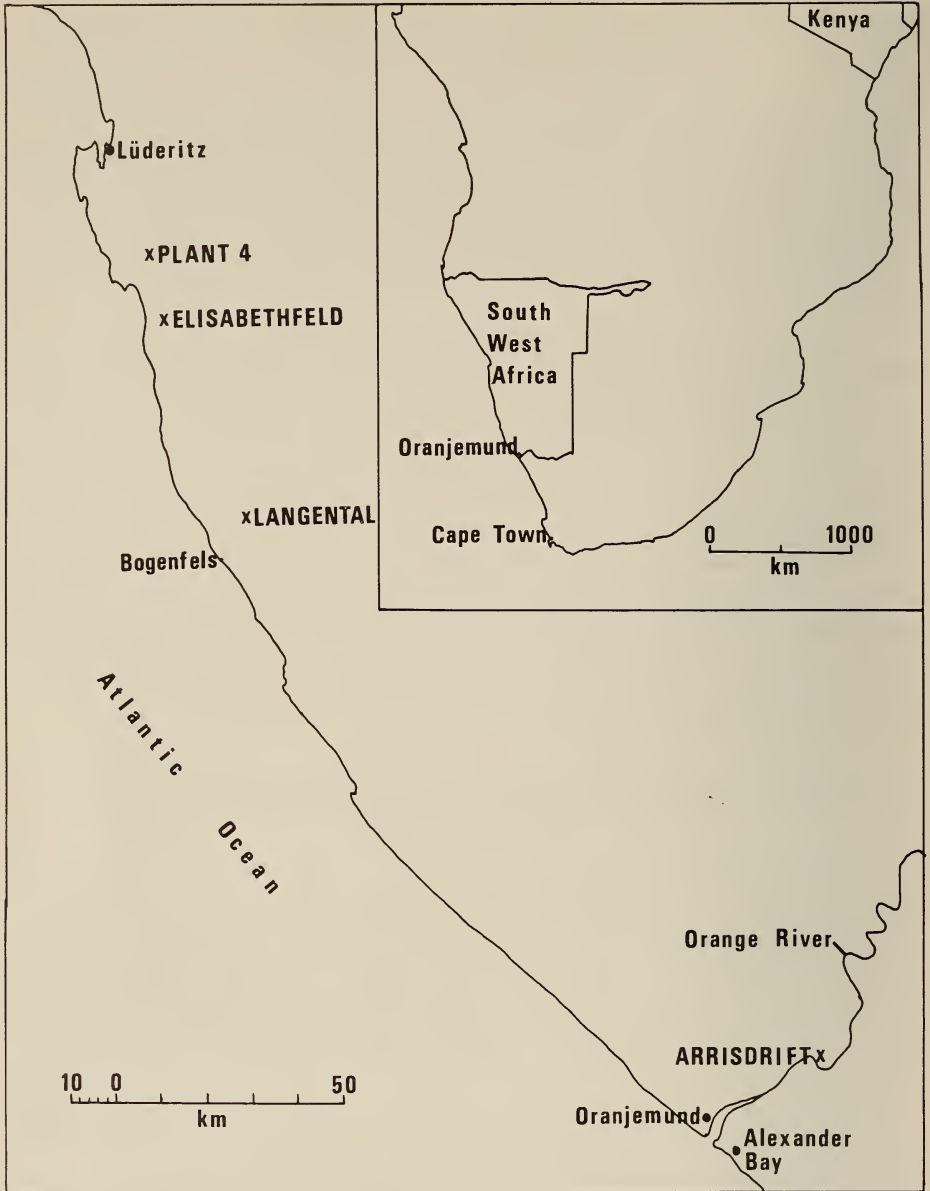
Fig. 1. Location of Arrisdrift and other South West African Miocene fossil occurrences.

Hamilton & Van Couvering (1977) recently revisited the area and collected more material from the various localities. They have reviewed and supplemented the original faunal lists and compared and contrasted a revised list with others from early Miocene occurrences elsewhere in Africa.

The Namib fossils are generally regarded as early Miocene ('Burdigalian') in age, their source is usually recorded as 'Namib desert' or 'South West Africa', and they are treated as if they were a single assemblage. The described material is here listed as four separate assemblages (Table 2). Since each is limited in size and each includes unidentified or incompletely identified taxa, the bases for comparing them to each other, and to assemblages elsewhere, are limited. The comments which follow are confined largely to the implications of individual taxa in respect of the age of the assemblages. Other references to this material are included in the discussions on the Arrisdrift fossils.

There is one species from Elisabethfeld, *Metapterodon kaiseri*, which Savage (1965) believed to be represented in east Africa by specimens from Karungu and Rusinga, which are between 18 and 20 m.y. old. Savage also recognized a second species of *Metapterodon* from Rusinga, namely, *M. zadoki*. Van Valen (1967: 252) found 'that the two east African species distinguished by Savage are much more similar to each other than are the east and Southwest African forms of "*M. kaiseri*"'. He concluded that the east African species are more advanced than *M. kaiseri* and synonymized *Metapterodon* with *Pterodon*. Although this material is problematical, Van Valen's opinion suggests that the Elisabethfeld species may predate its east African counterparts. Its age might therefore be greater than 20 m.y., that is, 'Aquitanian' rather than 'Burdigalian' in terms of the European mammal age nomenclature (Van Couvering 1972).

Another of the Elisabethfeld species, *Myohyrax doederleini*, was regarded as a synonym of the east African *M. oswaldi* (Whitworth 1954; Patterson 1965), a species which has a recorded age range of 18 to 22 m.y. (see Whitworth 1954; Walker 1969; Van Couvering 1972). An 'Aquitanian' to 'Burdigalian' age is therefore indicated. Since a *Myohyrax* resembling *M. oswaldi* is now also recorded from Arrisdrift, this species may have survived beyond the 'Burdigalian' (see below), and appears to be of little use for relative dating purposes.

The Elisabethfeld *Propalaeoryx austroafricanus* is a primitive ruminant which is likely to be broadly contemporaneous with the Rusinga *P. nyanzae* (Whitworth 1958; Hamilton 1973), but the available material of these species is too scanty to determine possible differences of temporal significance.

The only other identified species from Elisabethfeld are *Parapedetes namaquensis* and *Austrolagomys inexpectatus*. They are not known elsewhere, although there are related genera, *Megapedetes* and *Kenyalagomys*, recorded from the early Miocene of east Africa, again from the 18 to 22 m.y. period.

According to MacInnes (1957) *Megapedetes* is less specialised than *Parapedetes*, but he did not regard this as indicating an age difference, ascribing it instead to different evolutionary trends on two contemporary lineages. This interpretation raises the question of whether assemblages such as those from Elisabethfeld can be dated in a relative sense by comparing them with east African assemblages. If MacInnes's interpretation of the pedetids is correct, then it follows that seemingly primitive taxa such as *Pterodon kaiseri* may

TABLE 2. Miocene mammals from the Lüderitz/Bogenfels area of the Namib desert.

ELISABETHFELD[1]	PLANT 4 BOREHOLE[1]	LANGENTAL[1]	SOUTH OF LÜDERITZ[2]	REVISED IDENTIFICATIONS AND ADDITIONS[3]
Myohyrax doederleini	*Myohyrax oswaldi*	—	*Myohyrax doederleini*	*Myohyrax oswaldi*
			Myohyrax osborni	*Myohyrax oswaldi*
		Protypotheroides beetzi		*Protypotheroides beetzi*
				Protypotheroides beetzi
Metapterodon kaiseri				*Prerodon kaiseri*
Creodonta/Carnivora indet.				Creodonta/Carnivora indet.
		Prohyrax tertiarius		*Prohyrax tertiarius*
				Gomphotherium sp.
				Brachypotherium heinzelini
Artiodactyla indet.	Artiodactyla indet.	Rhinocerotidae indet.		Artiodactyla indet.
		Diamantohyus africanus		*Xenochoerus africanus*
		? *Propalaeochoerus* sp.		? *Propalaeochoerus* sp.
				Brachyodus africanus
			Tragulidae indet.	*Dorcatherium* sp.
			Tragulidae indet.	Pecora indet.
Propalaeoryx austroafricanus	? cf. *Strogulognathus* sp.	cf. *Strogulognathus* sp.		*Propalaeoryx austroafricanus*
				Propalaeoryx austroafricanus
Austrolagomys inexpectatus			*Austrolagomys simpsoni*	*Austrolagomys inexpectatus*
				Kenyalagomys simpsoni
Parapedetes namaquensis				*Parapedetes namaquensis*
	Bathyergoides neotertiarius	*Bathyergoides neotertiarius*		*Bathyergoides neotertiarius*
	Neosciuromys africanus	*Neosciuromys africanus*		*Paraphiomys pigotti*
	Phionyoides humilis			*Phionyoides humilis*
	cf. *Phionys andrewsi*			—
		Diamantomys luederitzi	*Apodecter stromeri*	*Diamantomys luederitzi*
		Pomonomys dubius	*Phthinylla fracta*	*Pomonomys dubius*
				Paraphionys stromeri
				Paraphionys pigotti
				Paracryptomys mackennae
Rodentia indet.	Rodentia indet.	Rodentia indet.	Rodentia indet.	Rodentia indet.

[1] Stromer (1926)   [2] Hopwood (1929)   [3] Hamilton & Van Couvering (1977); this report.

simply be conservative southern counterparts of 'advanced' east African species.

This problem arises again with the ochotonids. There are clear differences between *Austrolagomys* and *Kenyalagomys* (MacInnes 1953), which may be interpreted as indicating that the former is the more primitive (Cooke 1972). In this instance the fact that the ochotonid represented at Arrisdrift (which evidently does postdate both the Elisabethfeld and the east African 'Rusinga-type' faunas) is a *Kenyalagomys*, may be an indication that *Austrolagomys* really is a primitive and early form.

To sum up, there is some evidence to suggest that the Elisabethfeld fauna represents a southern African equivalent of that of the European Aquitanian. This conclusion is, however, tentative and should be re-examined if more material becomes available and/or when the zoogeographic relationships of east and southern African early Miocene faunas are better understood.

The Langental fauna includes five species which are known from the early Miocene of east Africa. They are *Bathyergoides neotertiarius*, *Paraphiomys pigotti*, *Diamantomys luederitzi* (Lavocat 1973), *Xenochoerus africanus* (Wilkinson 1976) and *Brachypotherium heinzelini* (Heissig 1971). In addition, *Prohyrax tertiarius* is a primitive species and apparently consistent with an early Miocene date (see p. 33). This hyrax is regarded as one of the more certain indications that there was some endemism in southern African faunas during the earlier part of the Miocene and that the complication in comparing east and southern African taxa mentioned above does have some substance.

The other identified taxa from Langental, *Protypotheroides beetzi* and *Pomonomys dubius*, are apparently known only from the Namib desert and, since they may be southern endemics, they may not be useful for relative dating purposes.

The available evidence indicates that the Langental fauna dates from the early Miocene and that it may be a 'Burdigalian' rather than 'Aquitanian' equivalent.

The Plant 4 borehole and Langental faunas have three species in common, namely, *Myohyrax oswaldi*, *Bathyergoides neotertiarius* and *Paraphiomys pigotti*. This suggests that the former may also be of early Miocene age. On the other hand, all three taxa are, or may be represented at Arrisdrift as well (see below), so a slightly younger age (early middle Miocene) is also possible.

The material described by Hopwood (1929) includes three species known from the east African early Miocene. They are *Paraphiomys pigotti*, *P. stromeri* and *Myohyrax oswaldi*. In addition, this assemblage includes an ochotonid which is apparently closely related to the east African *Kenyalagomys minor* (see p. 31). Hopwood's material also includes the large myohyracine, *Protypotheroides beetzi*, which is represented at Langental. Once again an early Miocene age is indicated. In view of the earlier comments on ochotonids, the presence of *Kenyalagomys* in Hopwood's assemblage may mean that this assemblage, or part of it, postdates that from Elisabethfeld.

In spite of the uncertainties relating to the four assemblages, there is no

justification for the recent practice of treating the faunas as a unit. Even if it could be established that they are exact contemporaries, it is as well to accord them individual status. Since the Arrisdrift fauna is younger than some or all of those from the Lüderitz–Bogenfels area, there is certainly no justification for adding it to the Namib Miocene mixture, and for this reason alone it will now be inconvenient and inappropriate to refer to '*the* Miocene fauna' from this region.

THE FOSSIL VERTEBRATES FROM ARRISDRIFT

CLASS OSTEICHTHYES

One or more species of fish are represented by a few isolated vertebrae (e.g. AD 668, AD 672) and fin spines (e.g. AD 759, AD 779). The latter apparently belong to catfish (Clariidae).

CLASS AMPHIBIA

A single postcranial bone (AD 811) belongs to a frog or toad.

CLASS REPTILIA

ORDER SQUAMATA

There are two snake vertebrae (AD 707, AD 1110) in the assemblage.

ORDER CROCODILIA

? *Crocodylus niloticus* Laurenti, 1768

The most commonly represented lower vertebrate is a crocodile, probably *Crocodylus niloticus*, of which many isolated teeth (e.g. AD 71, AD 310) and scutes (e.g. AD 335, AD 341) are preserved. Postcranial bones and skull fragments are less common. The best specimens include two incomplete dentaries (AD 344, AD 999). Crocodiles are not uncommon as fossils in east Africa and elsewhere but have not previously been recorded from Tertiary occurrences in southern Africa and are rare in Quarternary deposits.

ORDER CHELONIA

A few isolated scutes (e.g. AD 73, AD 832) belong to one or more species of tortoise.

CLASS AVES

Birds are represented by a few isolated and incomplete postcranial bones (e.g. AD 725, AD 841) belonging to more than one species.

CLASS MAMMALIA

ORDER INSECTIVORA

Family **Macroscelididae**

Myohyrax cf. *oswaldi* Andrews, 1914

A *Myohyrax* is the most commonly occurring small mammal in the assemblage and is represented by many isolated teeth and mandible fragments (e.g. AD 125, AD 1104) (Fig. 2). Most of the mammalian postcranial bones have yet to be classified and this material probably includes specimens belonging to *Myohyrax*.

Stromer (1926) recorded three myohyracines from the Namib, namely, *M. oswaldi*, *M. doederleini* and *Protypotheroides beetzi*, while Hopwood (1929) subsequently named an additional species, *M. osborni*, from the same region. In the most recent review of this material, Patterson (1965) recognized only *M. oswaldi* (including *M. doederleini*) and *P. beetzi* (including *M. osborni*). In doing so he followed Whitworth (1954), except that Whitworth did not regard *Protypotheroides* as a valid genus.

The Arrisdrift *Myohyrax* is apparently indistinguishable from *M. oswaldi*, but the identification is qualified since the teeth are a little smaller than those
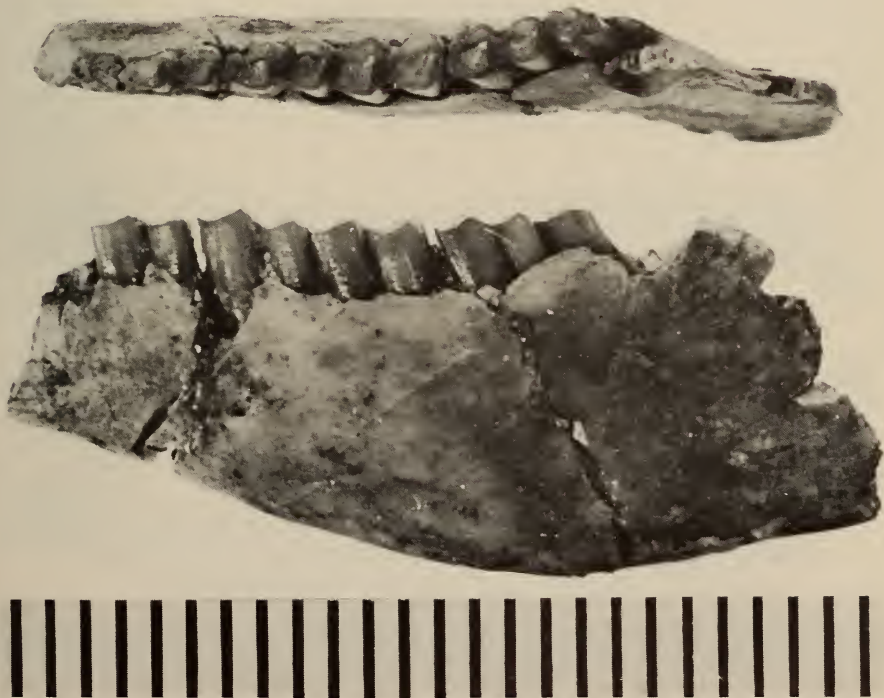

Fig. 2. Occlusal and buccal views of *Myohyrax* cf. *oswaldi* mandible (AD 971) from Arrisdrift.

of typical east African *M. oswaldi*. This was one of the features which Stromer (1926) claimed characterized *M. doederleini*. Whitworth (1954) found that *M. doederleini* fell within the size variation observed in east African *M. oswaldi*, but since Arrisdrift provides a second sample of specimens from the Namib in which the teeth are comparatively small, there may be a taxonomically significant mean difference between the *Myohyrax* from the two regions. In addition, since examination of the Arrisdrift *Myohyrax* during the present study was cursory, the material may differ from typical *M. oswaldi* in characters other than size.

The Arrisdrift *Myohyrax* is evidently younger than any previously recorded myohyracine (see p. 32), and this is another factor to be taken into account when the material is studied in detail.

ORDER CARNIVORA

Although poorly represented, the only identifiable carnivores from Arrisdrift are Carnivora rather than Creodonta. It is, however, possible that certain non-diagnostic specimens such as isolated canines and postcranial bones do belong to creodonts, a group whose presence is to be expected in view of the apparent age of the Arrisdrift assemblage (see p. 35).

Family **Amphicyonidae**

Amphicyon cf. *steinheimensis* Fraas, 1885

An incomplete left mandible (AD 133) belongs to an amphicyonid (Fig. 3, Table 3). There are also several postcranial bones which may belong to this

Fig. 3. Occlusal and buccal views of *Amphicyon* cf. *steinheimensis* mandible (AD 133) from Arrisdrift.

TABLE 3

Dimensions of the lower teeth and mandibles of the unidentified large carnivore (AD 1520), *Amphicyon* (AD 133), Hemicyoninae indet. (AD 611) and *? Ischyrictis* (AD 614) from Arrisdrift.

	$\bar{C}$		P_1		P_2		P_3		P_4		M_1		M_2		M_3	
	l	b	l	b	l	b	l	b	l	b	l	b	l	b	l	b
AD 1520	—	—	—	—	—	—	c. 20,0*	—	21,7	14,2	36,0	19,5	c. 26,0	21,1	c. 16,0*	—
AD 133	16,2	10,4	5,5*	—	7,2*	—	c. 9,0*	—	14,6	7,6	27,1	12,2	16,5	11,7	10,8	8,2
AD 611	—	—	c. 3,0*	—	8,5*	—	13,6*	—	17,5*	—	—	—	—	—	—	—
AD 614	c. 8,1	5,5	2,7*	—	5,7	3,0	6,5	3,4	9,0	4,3	14,6	6,3	c. 3,5*	—	—	—

* Alveolus

	AD 1520	AD 133	AD 611	AD 614
Depth of mandible below P_3	60,2	32,5	45,0	14,9
Breadth of mandible below P_3	30,3	13,5	18,5	7,6
Depth of mandible below M_1	62,6	38,0	54,5	c. 15,5
Breadth of mandible below M_1	29,0	c. 16,0	21,5	9,3

species, but they were excluded from consideration.

The amphicyonids, which are sometimes regarded as a subfamily within the Canidae (e.g. Kuss 1965), or as a separate family (e.g. Hunt 1972), were a successful, diverse and widespread group in the Old World and North America during the Oligocene and Miocene. They are not well known in Africa and prior to the Arrisdrift discovery had not been recorded in southern Africa. The taxonomy of the group is complex and, in spite of recent revisions, the identification of specimens such as AD 133 is difficult.

AD 133 lacks the ascending ramus, the incisors and P_1 to P_3. Of the remaining teeth only the M_3 is largely intact, although the salient features of the $\overline{C}$ and P_4 to M_2 are preserved. This specimen indicates that the species was an unspecialized, slender-jawed *Amphicyon* of moderate size. The P_1 to P_3, of which only the roots or alveoli remain, are reduced in size and more or less evenly spaced between the C and P_4. The P_1 was single-rooted, P_2 had two roots which has coalesced at the alveolar margin, while P_3 was also double-rooted. The P_4, which has lost the principal cusp, has an anterior accessory cusp, a larger posterior accessory cusp and a tiny cusp on the posterior cingulum. The M_1 is a high-crowned tooth with a prominent protoconid and stout metaconid. The talonid is sectorial, it lacks the entoconid and makes up about one-third of the length of the tooth. The M_2 has a double-cusped trigonid and single-cusped talonid. The M_3 has little relief on the occlusal surface and, like M_1 and M_2, is relatively narrow.

AD 133 resembles specimens belonging to the middle Miocene *A. steinheimensis* from Europe (see Kuss 1965), and is tentatively identified with this species. It may, however, belong to a previously unrecorded African species of *Amphicyon*. The only amphicyonids recorded from east Africa are two early Miocene species, *Hecubides euryodon* and *H. macrodon* (Savage 1965). The Arrisdrift species differs from *H. eurydon* in several respects, including its larger size. It cannot be compared with *H. macrodon*, which is known only from an isolated M^1.

<p align="center">Superfamily Canoidea (senso Savage 1977)</p>

<p align="center">Amphicyonidae or Hemicyoninae gen. et sp. indet.</p>

A largely intact, but somewhat abraded right mandible with well worn P_4 to M_2 (AD 1520) belongs to a very large canoid (Fig. 4). This specimen compares in size with the mandible of the largest terrestrial carnivore previously recorded from southern Africa, namely, the early Pliocene *Agriotherium africanum* from Langebaanweg, Cape Province (Hendey 1972, 1977).

In some respects AD 1520 resembles the European middle to late Miocene amphicyonid, *Amphicyon major*. For example, the mandibles of the two species are of similar overall size, while the preserved teeth of AD 1520 are morphologically similar to the corresponding teeth of *A. major*. Like all amphicyonids, AD 1520 lacks a premasseteric fossa. Its teeth are closest in size to those of
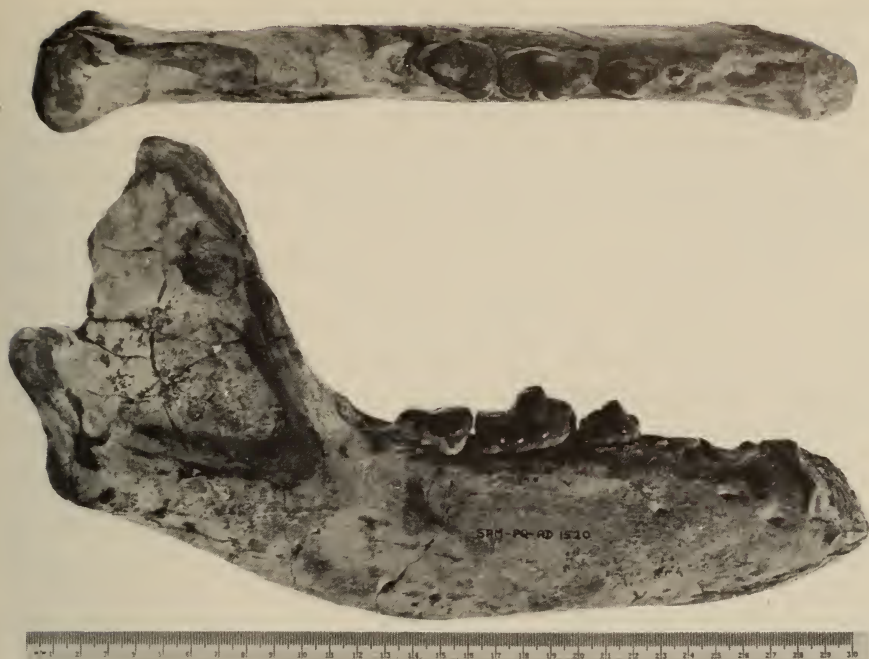
Fig. 4. Occlusal and buccal views of large canoid mandible (AD 1520) from Arrisdrift.

later varieties of *A. major* (see Kuss 1965; Table 3, this report). They do, however, differ in being relatively broad, a feature which applies particularly in the case of P_4. Although lost, the P_2 and P_3 of AD 1520 were evidently also relatively large and, together with P_4, formed a closed series.

The large size of the premolars distinguishes the Arrisdrift species from previously recorded *A. major* and, indeed, from all other Miocene amphicyonids. Apparently only in certain Oligocene species are the premolars relatively large and in the form of a closed series (see Springhorn 1977). If AD 1520 is indeed related to *A. major*, it must be more primitive than recorded representatives of this taxon even though it is 'advanced' in terms of overall size. The origins of *A. major* are obscure (Kuss 1965) and it may well have arrived in Europe as an immigrant from Africa. The Arrisdrift species may represent the stock from which *A. major* was derived.

There is, however, a second alternative which must be considered. The Hemicyoninae, a group of Miocene ursids which share many characters with amphicyonids, also include a very large species whose origins are obscure. This is *Dinocyon thenardi* of the later middle Miocene of Europe (Hürzeler 1944). The hemicyonines also have reduced premolars, although the reduction is not necessarily as marked as in contemporary amphicyonids. They presumably evolved from forms in which the premolars were relatively large and

in this respect the Arrisdrift species may be seen as an appropriate ancestor for *D. thenardi*. The lower molars of the former are a little smaller than those of the Grive St Alban *D. thenardi*, and in this respect as well the Arrisdrift species is the less specialized (i.e. more primitive).

AD 1520 does, however, differ from *D. thenardi*, and other hemicyonines, in lacking a premasseteric fossa. This would not necessarily exclude it from an ancestral role, but it does suggest an amphicyonid, rather than hemicyonine connection.

A third alternative is that the Arrisdrift species represents the stock from which both *A. major* and *D. thenardi* were derived. It has been suggested that *Amphicyon* and *Dinocyon* are closely related (e.g. Matthew 1924), although more recent interpretations of canoid inter-relationships indicate that similarities between these taxa are due to parallel evolution. Nevertheless, the fact that neither *A. major* nor *D. thenardi* have known immediate ancestors does raise the possibility that they may have had one in common.

Finally, AD 1520 may belong to a species related to the early Miocene *Afrocyon burolleti* from Gebel Zelten in Libya (Arambourg 1961). The holotype of this species is a mandible fragment with P_4 to M_3, which is similar in overall size to AD 1520, but which differs in having smaller P_4 to M_2 and a double-rooted M_3. If the two forms are indeed related, then *A. burolleti* is clearly the more primitive and the Arrisdrift species could still be ancestral to the European *A. major* and/or *D. thenardi*.

In view of the uncertainties about the relationships of AD 1520, it would be fruitless at this stage to consider the taxonomic implications of the various alternatives mentioned above. Although unidentified, AD 1520 is still significant in revealing the presence of a type of carnivore not hitherto known from the Miocene of southern Africa and in suggesting that the phylogeny of similar taxa elsewhere may require reinterpretation.

? Family **Ursidae**

? Hemicyoninae gen. et sp. indet.

A mandible fragment (AD 611) belongs to a carnivore intermediate in size between the *Amphicyon* cf. *steinheimensis* and the large canoid discussed above (Table 3). Only the anterior part of the mandibular corpus is preserved, and of the teeth only the roots or alveoli of P_1 to P_4 and a small part of the crown of M_1 are preserved. It is readily distinguished from the *Amphicyon* cf. *steinheimensis* by its larger size and in having a deep mandibular corpus. In the latter respect it resembles the large canoid, but the overall size difference is more than would be expected in intra-specific variation.

Although AD 611 has yet to be positively identified, it matches in size and other observable respects corresponding parts of the *Hemicyon californicus* holotype from the Miocene of North America (Frick 1926: 34, fig. 12B). It is larger than specimens of European *Hemicyon* and *Harpaleocyon* described by

Hürzeler (1944), but since hemicyonines and other ursids exhibit appreciable sexual dimorphism (see Colbert 1939), size differences are not necessarily a reliable criterion for distinguishing species. Even if it could be established that AD 611 represents a hemicyonine, it is unlikely that the species concerned could be identified.

Hemicyonines have not previously been recorded from Africa, but elsewhere they occur in association with some of the characteristically Miocene taxa which have been found at Arrisdrift. The size of AD 611 suggests a middle Miocene rather than earlier age.

? Family **Felidae**

? *Metailurus* sp.

An isolated upper canine (AD 616) apparently belongs to a large felid of the group which includes the extinct genera *Metailurus* and *Dinofelis*. The specimen is 16 mm long, 12,6 mm wide and has a crown height of 44 mm.

The species concerned was larger than the only *Metailurus* hitherto recorded in Africa, namely, *M. africanus* from the east African early Miocene (Savage 1965). AD 616 compares in size with the $\underline{C}$ of *M. major* from the late Miocene of China (Zdansky 1924), but differs in being slightly shorter and broader. It also resembles the $\underline{C}$ of the early Pliocene *Dinofelis* aff. *diastemata* from Langebaanweg (Hendey 1974), particularly the specimen SAM–PQ–L 20685. Once again the only difference is that AD 616 is a little shorter and broader. This difference suggests that the Arrisdrift species was less advanced than the other two species.

Since carnivore canines are not necessarily diagnostic, AD 616 is only tentatively identified and is referred to *Metailurus*, a Miocene genus, rather than *Dinofelis*, a Plio/Pleistocene genus, in view of the age of the Arrisdrift assemblage.

Family **Mustelidae**

? *Ischyrictis* sp.

An incomplete left mandible (AD 614) belongs to a small carnivore with a high-crowned canine, relatively narrow and high-crowned premolars and carnassial, and a reduced M_2 (Fig. 5, Table 3). The M_1 has a small metaconid, while the talonid is short and lacks the entoconid. The small M_2 and sectorial M_1 talonid suggests that the relationships of AD 614 may lie with the primitive gulonine *Ischyrictis* and it is identified accordingly. This genus has not previously been recorded in Africa, but is known from the Miocene of Europe and Asia Minor (see Crusafont-Pairo 1972; Schmidt-Kittler 1976).

The high-crowned teeth and relatively narrow premolars of AD 614 would be primitive characters in an *Ischyrictis*, and the Arrisdrift species may prove to be an appropriate ancestor for the early Vindobonian *I. zibethoides* of Europe.
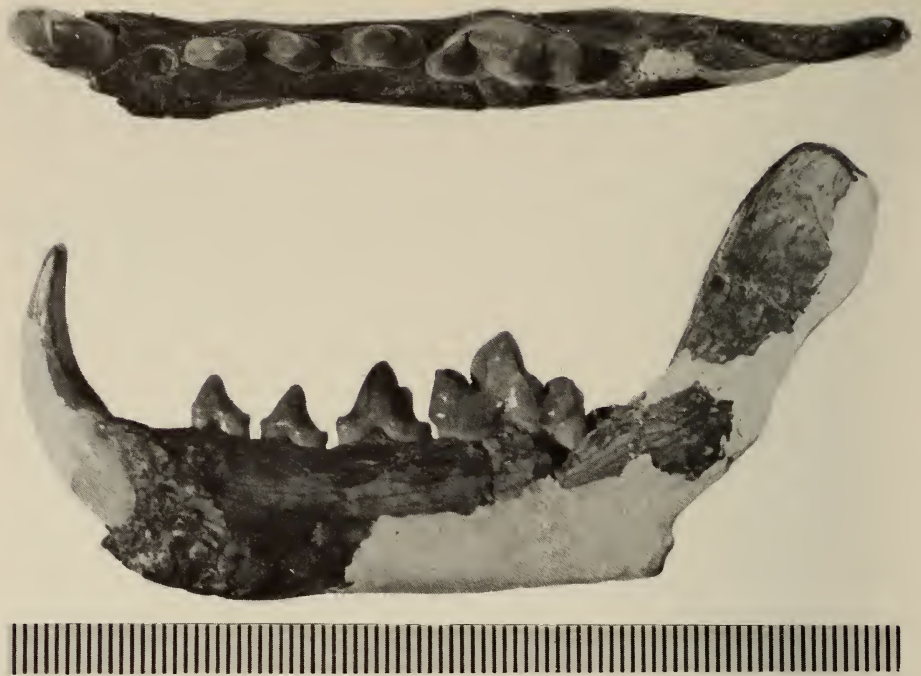
Fig. 5. Occlusal and lingual views of *? Ischyrictis* mandible (AD 614) from Arrisdrift.

Two other mandible fragments (AD 128, AD 756) apparently belong to the same species as AD 614.

Other Carnivora

At least one species in addition to those already mentioned is included in the Arrisdrift carnivore assemblage. An isolated canine (AD 127) belongs to a species smaller than the *? Ischyrictis*. The 'Carnivora gen. et sp. indet.' in the accompanying faunal list (Table 1) refers to this specimen.

Also unidentified are two mandible fragments (AD 139, AD 773), three canines (AD 55, AD 122, AD 214), an I³ (AD 619) and several postcranial bones, most of which are incomplete. These specimens may include some belonging to species in addition to those listed.

ORDER HYRACOIDEA

Family **Procaviidae**

Prohyrax sp. nov.

By far the most commonly represented vertebrate in the Arrisdrift assemblage is a hyrax belonging to a group sometimes given subfamily rank, the Pliohyracinae (Whitworth 1954). This was the most widespread of the hyrax

groups and is known from localities in Eurasia as well as Africa. Most of the recorded species were extremely large in comparison to living hyracoids and some specimens have been mistakenly identified as rhinoceroses and chalicotheres. Later representatives were apparently aquatic or amphibious animals (see Osborn 1899; Vekua 1972).

As here understood, the Pliohyracinae include the following genera:

Prohyrax—relatively small; early to middle Miocene of South West Africa (Stromer 1923, 1926; this report)

Parapliohyrax—large; middle to late Miocene of east and north Africa (Lavocat 1961; Bishop & Pickford 1975)

Pliohyrax—very large; late Miocene and Pliocene of Europe and China (Forsyth-Major 1899; Osborn 1899; Viret 1949; Viret & Thenius 1952; Tung & Huang 1974)

Kvabebihyrax—very large; late Miocene of the Soviet Union (Gabunia & Vekua 1966)

Postschizotherium—very large; late Miocene and Pliocene of China (Von Koenigswald 1966; Tung & Huang 1974)

The relationships of *Prohyrax tertiarius* from Langental have hitherto been obscure since it has been known only from fragmentary material, the holotype being a maxillary fragment with P^3 to M^2 and part of M^3 (Stromer 1926: Pl. 41, fig. 33). Only limited comparisons with the abundant Arrisdrift material are therefore possible, but there can be little doubt that the two forms are closely related. They are probably not conspecific since the Arrisdrift material belongs to a larger species, but they are here taken to be congeneric. Since the Arrisdrift species is undoubtedly a pliohyracine, *Prohyrax* is accordingly included in this subfamily.

The Arrisdrift species shares some characters with other pliohyracines but it is not conspecific with any of them, the most obvious difference being its smaller size. It is apparently closest to the east and north African *Parapliohyrax* and differs appreciably from the three Eurasian genera, which are the youngest and most highly specialized members of the group.

The Arrisdrift hyrax is here interpreted as a new species of the genus *Prohyrax*, probably directly descended from the Langental *P. tertiarius* and a likely ancestor of the later pliohyracines from further north in Africa and from Eurasia.

Although the species will be dealt with in detail elsewhere, some observations on it are included here since it is such an important element in the Arrisdrift assemblage.

More than forty individual animals of all ontogenetic ages are represented, mainly by mandible and maxilla fragments, although isolated teeth and postcranial bones are not uncommon. The best specimen is a nearly complete skull (AD 363) which lacks only the mandible, right I^2, left M^1, and parts of the right M^3 and right zygomatic arch (Fig. 6, Table 4). The skull is slightly distorted

Fig. 6. Dorsal, lateral and ventral views of *Prohyrax* skull (AD 363) from Arrisdrift.

TABLE 4

Dimensions of the *Prohyrax* skull (AD363) from Arrisdrift.

Overall length	160,8
Condylobasal length	152,0
Palate length along midline	97,7
Anterior margin of orbit to anterior margin of I^1	68,0
I^1 to M^3 length	96,9
P^1 to P^4 length	32,9
M^1 to M^3 length	c. 47,5
M^3 length	24,7
M^3 breadth	17,3
Interorbital width	36,7
Postorbital width	37,1
Zygomatic width	91,0
Mastoid width	73,8
Palate width at M^3	26,3
Horizontal diameter of orbit	24,3
Vertical diameter of orbit	21,0
Ventral margin of orbit to M^3 alveolar margin	18,7

in places, particularly the posterior part of the braincase. Distinctive features, some of which are characteristic of other pliohyracines, include closed orbits, naso-maxillary fossae which lead ventrally and posteriorly into antorbital foramina situated immediately above the infraorbital foramina, a dental formula of 3.1.4.3 with the I^2 to M^3 series closed, a premolariform $\underline{C}$ and an elongated M^3 with an additional (third) lobe situated posteriorly. The preceding comments on the upper teeth also apply to the lowers. The mandibles lack the fossae and fenestrae found in some other Tertiary hyracoids.

Apart from its smaller size, the Arrisdrift species is most readily distinguished from later pliohyracines by its less elevated orbits and narrower skull.

ORDER PROBOSCIDEA

Family **Gomphotheriidae**

Gen. et sp. indet.

Four largely intact molars and a premolar (e.g. AD 252, AD 257) belong to at least three individuals of an unidentified gomphothere (Fig. 7). They resemble, and may be conspecific with, specimens from Maboko in Kenya which date back about 16 m.y.

This material was originally identified by MacInnes (1942) as *Trilophodon angustidens kisumuensis*. Arambourg (1945) believed that two taxa were represented and named a new genus and species, *Protanancus macinnesi*, to accommodate some specimens. Subsequently Tobien (1973) suggested that the Maboko material belongs to a *Platybelodon* (*P. kisumuensis*), while Maglio (1974) referred it to *Gomphotherium* cf. *angustidens*. Recently Tassy (1977) identified it with *Choerolophodon* (*C. kisumuensis*).

This diversity of opinion is an indication of the difficulties which exist in identifying fragmentary proboscidean remains, and it was decided to withhold

Fig. 7. Occlusal view of Gomphotheriidae third molar (AD 257) from Arrisdrift.

even a tentative identification of the Arrisdrift species. It is, however, unlikely to be a *Platybelodon* since none of the numerous tusk fragments from Arrisdrift are of the *Platybelodon* type.

Even though the material is unclassified, it is important since the molars are more advanced than those of early Miocene gomphotheres elsewhere and they are one of the elements in the assemblage which suggest a late 'Burdigalian' or post-'Burdigalian' age for the fauna.

Family **Deinotheriidae**

Prodeinotherium hobleyi (Andrews, 1911)

The Arrisdrift deinothere is represented by three cheekteeth which have been described by Harris (1977).

Other Proboscidean Material

In addition to the cheekteeth already mentioned, there are many tusk fragments and a few postcranial bones which evidently belong to either the gomphothere or the deinothere. They have yet to be studied.

ORDER PERISSODACTYLA

Family **Rhinocerotidae**

Dicerorhinus sp.

At least three individuals of a rhinoceros are represented by several isolated cheekteeth (e.g. AD 635, AD 827) and postcranial bones (e.g. AD 251, AD 601), the latter being mainly elements of the pes.

The metatarsals which are known are relatively long compared with those of the living *Diceros bicornis* and *Ceratotherium simum*, which suggests that

Fig. 8. Occlusal and buccal views of *Dicerorhinus* M³ (AD 339) from Arrisdrift.

the species concerned was either an *Aceratherium* or a *Dicerorhinus* (see Hooijer 1966) (Table 5). The cheekteeth of African Miocene representatives of these genera may be difficult or impossible to distinguish (Hooijer 1966, 1968*a*), but two M³'s from Arrisdrift (AD 339, AD 1103) resemble those of *Dicerorhinus* rather than *Aceratherium* in having metacone bulges and unconstricted protocones (Fig. 8). These characteristics, together with the elongated metatarsals, distinguish the Arrisdrift species from other recorded African Miocene rhinoceroses, namely, *Paradiceros*, *Brachypotherium* and *Chilotheridium* (Hooijer 1966, 1968*b*, 1971).

Several Miocene species of *Dicerorhinus* have been recorded in Eurasia and Africa (Hooijer 1966), including *D. leakeyi* from the east African early Miocene. The teeth of the Arrisdrift species are larger than those of *D. leakeyi* and in this respect resemble the European middle Miocene *D. schleiermacheri* from Eppelsheim (Table 6). The Arrisdrift metatarsals are longer than those of *D. leakeyi*, which are themselves 'remarkable for their length' (Hooijer 1966: 178), and although the metatarsals of *D. schleiermacheri* are not known, Hooijer believed that they probably 'exceeded those of *D. leakeyi* in length'. Once again a similarity between the Arrisdrift and Eppelsheim species is indicated.

The Arrisdrift species may also be more advanced than *D. leakeyi* in having a less prominent metacone bulge, but there is doubt as to how much significance should be attached to variations in this feature (Hooijer 1966: 128).

The available rhinoceros material from Arrisdrift is probably inadequate for identifying the species concerned, but it does suggest one which was not conspecific with the early Miocene *D. leakeyi* and which was perhaps closer to the middle Miocene *D. schleiermacheri* in an evolutionary sense.

TABLE 5

Dimensions of *Dicerorhinus* metatarsals from Arrisdrift.

	AD251 Mt II	AD249 Mt III	AD253 Mt IV
Median length	177	190	170
Proximal width	33	61	43
Proximal antero-posterior diameter	48	—	—
Middle width	30	50	—
Middle antero-posterior diameter	25	26	—
Ratio middle width/length	0,17	0,26	—

All measurements approximte owing to condition of specimens.

TABLE 6

Dimensions of *Dicerorhinus* M³'s from Arrisdrift.

	AD339	AD1103
Antero-posterior diameter	55,0	54,3
Transverse diameter	61,0	54,1
Length of outer surface	65,9	66,3

ORDER ARTIODACTYLA

Family **Suidae**

Gen. et sp. indet.

A mandible fragment with two cheekteeth (AD 631) belongs to a small suid whose identity has yet to be determined.

Family **Suidae**

Lopholistriodon moruoroti Wilkinson, 1976

Several specimens belong to a small listriodont pig. They include a maxilla fragment with P^4 to M^3 (AD 136) and two isolated M_3's (AD 135, AD 636) (Fig. 9, Table 7).

TABLE 7

Dimensions of *Lopholistriodon moruoroti* teeth from Arrisdrift.

	P^4		M^1		M^2		M^3		M_3	
	l	b	l	b	l	b	l	b	l	b
AD 136 . .	6,5	8,3	9,0	9,2	10,3	10,4	11,4	10,1	—	—
AD 135 . .	—	—	—	—	—	—	—	—	14,0	7,9
AD 636 . .	—	—	—	—	—	—	—	—	12,4	8,1

In an unpublished thesis, Wilkinson (1972) described and named a new species of pig, *Xenochoerus ? moruoroti*, from Moruorot Hill in Kenya. He subsequently referred it to the genus *Lopholistriodon* Pickford & Wilkinson, 1975 (Wilkinson 1976). The teeth of the Arrisdrift listriodont are virtually indistinguishable from those of the Moruorot *L. moruoroti* and it is identified accordingly.

According to Pickford & Wilkinson (1975) this species is present at Moruorot (17 m.y.), Maboko (16 m.y.) and Muruyur (13 m.y.), so its presence at Arrisdrift is taken as a further indication that this fauna is late 'Burdigalian' or post-'Burdigalian' in age.

Family **Tragulidae**

Dorcatherium cf. *pigotti* Whitworth, 1958

Two mandible fragments (AD 104, AD 262) and a few postcranial bones belong to a small tragulid. The teeth are morphologically indistinguishable from those of *Dorcatherium* and, of the African species of this genus, they are closest in size to those of *D. pigotti* of the east African early Miocene (Whitworth 1958) (Table 8).

TABLE 8

Dimensions of *Dorcatherium* teeth from Arrisdrift.

	P_2		P_3		M_1		M_2	
	l	b	l	b	l	b	l	b
AD104	6,9	2,4	7,9	3,0	—	—	—	—
AD262	—	—	—	—	8,5	5,5	9,1	6,2

Fig. 9. Occlusal and buccal views of *Lopholistriodon moruoroti* maxilla (AD 136) from Arrisdrift.

The Arrisdrift specimens are only tentatively identified with this species since the grounds for distinguishing poorly represented fossil tragulids are limited. There is little variation in tooth morphology and there has been a tendency to name distinct species in Europe, Asia and Africa on the basis of size differences. It is by no means certain that similarly sized species on the different continents represent different species.

Family **Palaeomerycidae** (*senso* Hamilton 1973)

Climacoceras sp. nov.

The Arrisdrift ruminant assemblage includes several fragments of antler-like frontal appendages (ossicones) (e.g. AD 130, AD 132) (Fig. 10). The beams of the 'antlers' are straight, transversely compressed, and have small knobs situated at irregular intervals both anteriorly and posteriorly. They evidently also carried some small tines, several detached specimens having been discovered (e.g. AD 129, AD 785). The tines are circular in cross-section and slightly curved. AD 648 indicates that there was bifurcation and greater flattening of the 'antlers' distally. AD 483 apparently represents the proximal part of an 'antler' and since it lacks a burr, the 'antlers' were evidently not deciduous. They were, therefore, not true antlers of the kind which characterize the Cervidae.

Fig. 10. Lateral view of *Climacoceras* 'antler' fragments from Arrisdrift: AD 648 (+AD 763)—distal end showing bifurcation (left); AD 130—beam fragment showing knobs (centre); AD 129—tine (right).

The complete 'antlers' must have resembled those of *Climacoceras africanus* from Maboko (MacInnes 1936). *Climacoceras* is also present at Fort Ternan (Gentry 1970). The Arrisdrift specimens are distinguished from east African specimens by their larger size, the difference being of the order of 20 per cent according to A. W. Gentry (pers. comm.). The beam circumference of specimens from Maboko varies from 54 to 92 mm (MacInnes 1936), while the correspond-

ing figures for Arrisdrift specimens are 85 to 110 mm. The longest of the Maboko tines recorded by MacInnes measures 48 mm, whereas two of the Arrisdrift specimens (AD 129, AD 1177) are about 60 mm long and both are incomplete.

The larger size of the Arrisdrift specimens is taken to indicate that they belong to a hitherto unrecorded species of *Climacoceras*, although the morphological similarity to specimens from Maboko suggests that the Arrisdrift species was in a comparable evolutionary state to *C. africanus*.

Many mandible and maxilla fragments, isolated teeth and postcranial bones probably belong to this species. It is, however, not certain that all the material provisionally assigned to the *Climacoceras* belongs only to this species. A comparison between two of the more complete mandibles (AD 261, AD 612; Fig. 11, Table 9) revealed differences which may be taxonomically significant. For example, AD 612 has slightly larger teeth, an appreciably deeper mandibular corpus, larger basal pillars on the molars and a less expanded P_4 metaconid. In addition, the lingual surface of the M_3 third lobe is directly connected to the second and is flanked by a small, more or less circular enamel island which evidently corresponds to the central cavities of the first and second lobes. By contrast, the M_3 third lobe of AD 261 is transversely compressed dorsally and is connected lingually to the second lobe by a deeply indented loop in the enamel. It also lacks a 'central cavity'.

TABLE 9

Dimensions of lower teeth and mandibles AD 261 and AD 612, tentatively assigned to *Climacoceras* from Arrisdrift.

	P_3		P_4		M_1		M_2		M_3	
	l	b	l	b	l	b	l	b	l	b
AD 261	—	—	14,0	7,6	15,3	9,7	c. 17,5	12,5	24,0	9,5
AD 612	c. 15,5	c. 7,5	16,5	8,5	c. 17,0	—	21,3	c. 11,6	26,3	10,7

	AD 261	AD 612
Depth of mandible below P_4 . . .	25,0	29,0
Breadth of mandible below P_4 . . .	12,1	14,5
Depth of mandible below M_3 . . .	28,5	37,7
Breadth of mandible below M_3 . . .	13,0	15,8

Sorting the remaining mandible fragments on the basis of these criteria was not entirely satisfactory owing to the poor condition of some specimens and because in some instances 'characteristics' of one type occurred in conjunction with 'characteristics' of the second. Nevertheless, AD 259, AD 263, AD 269 and AD 270 are apparently of the AD 612 type and represent at least 4 individuals, while AD 271, AD 272, AD 346, AD 356 and AD 621 appear to be of the AD 261 type and represent 6 individuals.

The two sets of specimens are otherwise similar and amongst the shared characteristics are a giraffoid-like orientation of the diastema region relative to the cheektooth row, low-crowned cheekteeth, absence of P_1 and simple, crescentic central cavities on the lower molars, the posterior one opening

lingually in early wear. Although several symphyseal teeth are known, they do not include bilobed giraffoid-like canines.

The less numerous maxillae and upper teeth have not been closely examined. Gentry (pers. comm.) has found that although the large ruminant teeth and

Fig. 11. Occlusal and buccal views of *? Climacoceras* mandibles, AD 261 (above) and AD 612 (below), from Arrisdrift.

dentitions from Arrisdrift share several characters with the early Miocene *Propalaeoryx* from Elisabethfeld and the Fort Ternan *Climacoceras*, they are in some respects intermediate between the two. For example, the Elisabethfeld *Propalaeoryx* is more primitive in retaining P_1. On the other hand, at least some of the Arrisdrift M_3's (the AD 612 type) have 'central cavities' on the third lobes, whereas the Fort Ternan *Climacoceras* M_3's lack this feature. In addition, the Arrisdrift teeth are probably less high-crowned than those of the Fort Ternan *Climacoceras*, while the metastylids are developed to a degree intermediate between the Elisabethfeld and Fort Ternan species.

Since the Maboko *Climacoceras* predates the Fort Ternan species and is younger than the Elisabethfeld *Propalaeoryx*, a temporal link with the Arrisdrift species is suggested. Unfortunately the only described teeth assigned to the Maboko *Climacoceras* are three lower molars (MacInnes 1936), so the basis for comparisons with Arrisdrift specimens is limited. The Maboko teeth are, however, similar to the AD 261 type in size and some morphological characters, including reduced or absent basal pillars and dorsally compressed third lobe of M_3.

There are several complete specimens amongst the postcranial bones tentatively assigned to the *Climacoceras*. They include a tibia (AD 1100), several radii (e.g. AD 494, AD 562) and metapodials (e.g. AD 198, AD 199), as well as elements of the manus and pes. The long bones are slender and elongated compared with those of living bovids and cervids of similar overall size (e.g. *Damaliscus dorcas, Cervus unicolor*). The housing of the extensor tendon of the distal metatarsals shows the bovid and giraffid rather than the cervid condition (see Whitworth 1958: 23).

Family **Bovidae**

Gen. et sp. indet.

Several mandible fragments (e.g. AD 103, AD 106) and postcranial bones belong to a small ruminant (Fig. 12, Table 10). Morphologically the teeth are perhaps closest to those of the somewhat larger *Walangania africanus* (= *Palaeomeryx africanus* + *Walangania gracilis* (see Hamilton 1973)) of the east African early Miocene. *W. africanus* was once thought to be a bovid, but

TABLE 10

Dimensions of the lower cheekteeth and mandibles of the Bovidae indet. from Arrisdrift.

	P$_3$		P$_4$		M$_1$		M$_2$		M$_3$	
	l	b	l	b	l	b	l	b	l	b
AD 105 . .	7,8	4,2	8,3	4,8	—	—	9,4	6,7	13,0	6,5
AD 106 . .	—	—	8,1	4,5	9,1	6,3	9,7	6,6	—	—

	AD 105	AD 106
Depth of mandible below P$_4$ . . .	c. 12,4	14,3
Breadth of mandible below P$_4$ . . .	6,3	6,1
Depth of mandible below M$_3$ . . .	15,5	18,7
Breadth of mandible below M$_3$ . . .	7,6	7,9

Fig. 12. Occlusal and buccal views of Bovidae mandible (AD 105) from Arrisdrift.

Gentry (pers. comm.) now believes it could be congeneric with the primitive ruminant *Dremotherium* from the European late Oligocene to early Miocene.

Gentry (pers. comm.) reports on the Arrisdrift material as follows: 'The smaller metastylids of the lower molars are more advanced towards bovids than those of *Walangania*. Similarly, the weaker anterior ribs and the better developed closure of the central cavities. The Maboko bovid fragment with M_2 (see Whitworth 1958: 25, fig. 10a–c) appears to agree with the Arrisdrift species except in not being smaller than *Walangania*: its metastylid is weak, the anterior rib is not localized, and the central cavities are more enclosed within the tooth.'

He concludes that the Arrisdrift species 'is a bovid, although finding a horn core is needed to be conclusive'.

Other Ruminants

The possibility of a second taxon being represented amongst the material assigned to the *Climacoceras* has already been mentioned.

In addition, there are several ruminant postcranial bones which are too small to belong to the *Climacoceras*, but far too large to belong to the bovid. They include a distal humerus (AD 39), proximal metacarpals (AD 764, AD 964) and a first phalanx (AD 895). The 'Pecora gen. & sp. indet.' on the accompaying faunal list (Table 1) refers to this material

ORDER LAGOMORPHA

Family **Ochotonidae**

Kenyalagomys sp. nov.

A mandible fragment with M_1 and M_2 (AD 813) (Fig. 13) and an isolated P^3 (AD 1185) belong to a small ochotonid which resembles species previously
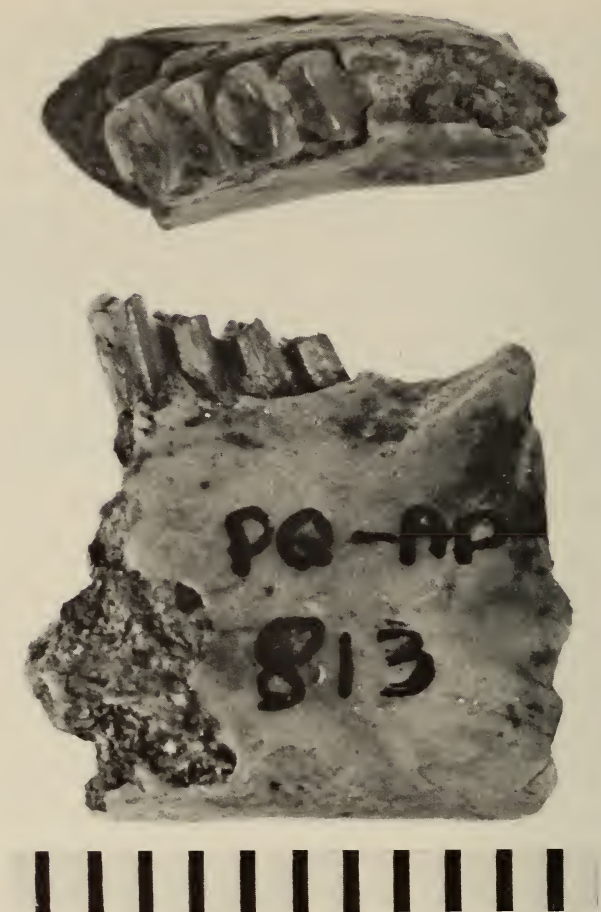
Fig. 13. Occlusal and buccal views of *Kenyalagomys* mandible (AD 813) from Arrisdrift.

recorded from early Miocene deposits in the Namib desert and east Africa.

The first African Miocene ochotonid to be described was *Austrolagomys inexpectatus* from Elisabethfeld (Stromer 1924, 1926). Hopwood (1929) recorded a second species from the same region, namely *A. simpsoni*. Subsequently MacInnes (1963) identified a second genus, *Kenyalagomys*, on the basis of material from east Africa and named two species, *K. rusingae* and *K. minor*.

MacInnes made no reference to Hopwood's species, but amongst the characters used to distinguish *Kenyalagomys* from *Austrolagomys* (MacInnes 1953: 20–21) are two of the three characters which distinguish *A. simpsoni* from *A. inexpectatus* (Hopwood 1929: 2). They are a deep external fold on P_3 and a marked median angulation (rib) on the posterior walls of the anterior lobes of P_4 to M_2. It follows that if the generic distinction is justified, and it is

here assumed that it is, then *A. simpsoni* must be referred instead to *Kenyalagomys*.

Judged on the basis of size, neither of the east African species is a synonym of *K. simpsoni*. *K. rusingae* is larger and, although *K. minor* is similar in overall size, it differs in having a smaller P₃ and larger molars.

Another species of *Kenyalagomys*, *K. mellalensis*, was recently recorded from the middle Miocene (*c.* 14 m.y.) of Beni Mellal in Morocco (Janvier & De Muizen 1976).

The molars of the Arrisdrift mandible (AD 813) are almost identical in size to the corresponding teeth of the *K. simpsoni* holotype, but the posterior walls of the anterior lobes lack the prominent ribs which characterize *Kenyalagomys*. There is, however, a faint indication of such ribs and the teeth of AD 813 are closer to the condition in *Kenyalagomys* than that in *Austrolagomys*, where the posterior walls are smoothly curved.

The Arrisdrift P³ (AD 1185), which measures 1,6 by 3,2 mm, is similar in size to that of *K. minor*, it is smaller than that of *K. rusingae* and longer, but narrower than that of *K. mellalensis*. It also resembles *K. minor* in having the postero-external corner pointed rather than rounded as in both *A. inexpectatus* and *K. rusingae*. *K. mellalensis* is in an intermediate position in this respect. AD 1185 differs from *K. minor* in having the posterior border more or less straight rather than convex and in this respect resembles *K. rusingae* and *K. mellalensis*. Visible on the occlusal surface is a deeply indented enamel fold which resembles corresponding features in the east and north African species of *Kenyalagomys*, but which is absent in *Austrolagomys*.

The Arrisdrift ochotonid is here regarded as a previously unrecorded species of *Kenyalagomys*, whose closest relatives are *K. minor* and *K. simpsoni*. If there is a phyletic relationship between the latter two species and the one from Arrisdrift, then the reduced median ribs of the anterior lobes of the lower molars of AD 813 may be interpreted as being either in an incipient or in a vestigial state. The latter alternative is more likely in view of the probable younger age of the Arrisdrift species relative to the Rusinga *K. minor* and its apparent contemporary from the Namib, *K. simpsoni*. Since *K. mellalensis* is more likely to be related to *K. rusingae* than the smaller African ochotonids, its evolutionary state relative to that of the Arrisdrift species is not determinable.

To sum up, the Arrisdrift ochotonid is apparently a new species of *Kenyalagomys* which is more advanced than the smaller species already recorded from the early Miocene of Africa.

ORDER RODENTIA

? Family **Bathyergidae**

? *Bathyergoides* sp.

Two incomplete lower incisors (AD 141, AD 1024) belong to a large rodent, possibly a bathyergid. They are tentatively attributed to *Bathyergoides*,

a genus recorded from the early Miocene of the Namib (Stromer 1926) and east Africa (Lavocat 1973).

<div align="center">Family Thryonomyidae</div>

<div align="center">Paraphiomys pigotti Andrews, 1914</div>

Two incomplete mandibles (AD 629, AD 1049) belong to a rodent which appears indistinguishable from that described by Stromer (1922, 1926) as *Neosciuromys africanus*. This taxon has since been recognized as a junior synonym of *Paraphiomys pigotti* by Lavocat (1973). *P. pigotti* is one of the more commonly occurring rodents in deposits of early Miocene age in both east Africa and the Namib desert. The Arrisdrift *P. pigotti* evidently postdates all previous records of this species (see below).

Other Rodents

The Arrisdrift assemblage includes many isolated rodent incisors and, judged on the basis of size, they represent at least two species in addition to those mentioned above.

AGE OF THE OCCURRENCE

The fauna from Pit 2/AD 8 at Arrisdrift undoubtedly dates from the Miocene and it has been suggested elsewhere (*South African Journal of Science* 1976; Corvinus & Hendey 1978) that it falls within the age limits of 12 to 18 m.y. The present study has tended to confirm the older limit, but it has also suggested that the 12 m.y. limit is too young.

At present the fauna can be dated only in a relative sense by comparing individual taxa with more securely dated ones elsewhere. The non-mammalian vertebrates cannot yet be used in this way and the comments which follow are confined to the mammals.

On the basis of previous records only two of the twenty-two mammalian species suggest an early Miocene date for the fauna. They are *Myohyrax* cf. *oswaldi* and *Paraphiomys pigotti*, which in east Africa are recorded from deposits ranging in age from 18 to 22 m.y. Since little has been published on the midde Miocene small mammals of east Africa, it cannot yet be assumed that these taxa did become extinct there 18 m.y. ago. In addition, since there is some evidence of differences in the patterns of mammalian evolution in east and southern Africa during the earlier part of the Miocene (see below), it is possible that taxa such as *M. oswaldi* and *P. pigotti* survived longer in southern Africa.

Two other species, the large canoid and *? Ischyrictis* sp., may also be indicative of an early Miocene date, but in both instances doubts about identification render them unreliable for relative dating purposes.

Five of the twenty-two species suggest a middle Miocene date, that is, late 'Burdigalian' at the earliest, but more probably 'Vindobonian' or even

'Maremmian' (*senso* Berggren & Van Couvering 1974). They are *Amphicyon* cf. *steinheimensis*, Gomphotheiidae indet., *Dicerorhinus* sp., *Lopholistriodon moruoroti* and *Climacoceras* sp. nov. In addition, there are another three species which are, or probably are, more advanced than previously recorded African 'Burdigalian' species and would be consistent with a middle Miocene date. They are *Prohyrax* sp. nov., Bovidae indet. and *Kenyalagomys* sp. nov. These eight species are regarded as the most significant for dating purposes.

Four of the twenty-two species would be consistent with any age from 'Burdigalian' to 'Vallesian'. They are ?Hemicyoninae indet., *? Metailurus* sp., *Prodeinotherium hobleyi* and *Dorcatherium* cf. *pigotti*.

The remaining six species provide no evidence of age. They are the unidentified carnivore, suid, pecoran and rodents.

Negative evidence also gives some indication of the probable age of the fauna. For example, the absence of equids suggests it is pre-'Vallesian' (see Hooijer 1975), while the absence of positively identifiable bovids and palaeotragines suggests that it predates the 14 m.y. old Fort Ternan fauna (see Gentry 1970; Churcher 1970).

There is, in fact, no secure evidence that the Arrisdrift fauna is as young as that from Fort Ternan, while there is good evidence that it postdates the 'Rusinga-like' faunas of east Africa. Consequently, the likely age limits may be reduced to between 14 and 18 m.y., with the median estimate being about 16 m.y. This is the age of the Maboko fauna and, although it has yet to be fully described, it includes at least six species which are conspecific with, or closely related to species from Arrisdrift (Table 11). They are *Choerolophodon kisumuensis*, *Prodeinotherium hobleyi*, *Lopholistriodon moruoroti*, *Dorcatherium pigotti*, *Climacoceras africanus* and the unidentified bovid. This suggests that the two faunas are, indeed, of the same order of age. On the other hand, the deinothere and tragulid are of little use as precise age indicators, while the two faunas do differ in certain respects. Primates and creodonts are absent or

TABLE 11

The mammals from Maboko, Kenya, and their counterparts from Arrisdrift, South West Africa.

MABOKO*	ARRISDRIFT
Primates	—
Paracynohyaeonodon leakeyi	Various Carnivora
Megalohyrax championi	*Prohyrax* sp. nov.
Choerolophodon kisumuensis	Gomphotheriidae indet.
Prodeinotherium hobleyi	*Prodeinotherium hobleyi*
Aceratherium acutirostratum	*Dicerorhinus* sp.
Lopholistriodon moruoroti	*Lopholistriodon moruoroti*
Brachyodus aequitorialis	—
Dorcatherium spp., including *D. pigotti*	*D.* cf. *pigotti*
Climacoceras africanus	*Climacoceras* sp. nov.
Bovidae indet.	Bovidae indet.

* Bishop (1967); Hooijer (1968*a*); Pickford & Wilkinson (1975); Tassy (1977); Van Valen (1967); Whitworth (1958).

apparently absent, at Arrisdrift and the hyracoids from the two occurrences are at least generically distinct. These differences will be discussed again later, but they indicate that either the two faunas were not exactly contemporaneous, or that there were regional differences between contemporary east and southern African faunas at that time.

The final word on the age of the Arrisdrift fauna has yet to come, but available evidence suggests that it is early middle Miocene, with an inferred date of about 16 m.y. before present.

PALAEOENVIRONMENT

The Arrisdrift fauna dates from a zoogeographically important period. Andrews & Van Couvering (1975: 85–87) have discussed the 'abrupt changes' which occurred in the faunas of east Africa between 14 and 18 m.y. ago and ascribe them to the development of a land bridge between Africa and Eurasia and the consequent immigration of new taxa. According to Berggren & Van Couvering (1974) the land bridge in question resulted from the closure of the eastern Tethys between 18 and 20 m.y. ago. Faunal changes must also have been experienced in southern Africa during this period, although it cannot be assumed that they were coincident with, or that they were an exact parallel of those in east Africa. There is, in fact, some evidence that the situation in southern Africa did differ from that in east Africa.

Andrews & Van Couvering (1975) pointed out that during the early Miocene the dominant hyracoids in east Africa were geniohyids and that they were replaced in the middle Miocene (post-Fort Ternan) by procaviids. In the Namib region the only recorded hyrax is the procaviid *Prohyrax*, which was contemporary with geniohyids in east Africa (up to and including Maboko). It follows that the procaviids are likely to have had southern Africa as their centre of origin and that they moved into east Africa at a time when this region was also receiving Eurasian immigrants. Even if there are changes in the classification of the hyracoid taxa concerned, the substance of the preceding theory remains the same since the east and southern African forms clearly belong to different lineages, and it is the southern African one (a pliohyracine) which had descendants in east Africa (and elsewhere) in post-early Miocene times.

Also relevant here is MacInnes's (1957) opinion that the southern African *Parapedetes* and east African *Megapedetes* were contemporary representatives of different lineages since it, too, suggests that there was some independent evolution of related taxa in the two regions. Other of the Namib rodents, as well as the ochotonid *Austrolagomys*, may also have been southern endemics.

In comparing faunas, it may be unwise to emphasize the absence of certain taxa since this may be due to sampling deficiencies or even incorrect identification of specimens. While the apparent absence of, for example, primates at Arrisdrift might be due to such factors, if their absence is real then it must be palaeoenvironmentally significant. The absence or great rarity of primates at

another southern African late Tertiary locality, namely, Langebaanweg, has already been mentioned elsewhere (Hendey 1976: 234), while this group is also not recorded from the other Miocene localities in the Namib.

By contrast, Andrews & Van Couvering (1975: 86) noted that during the early Miocene of east Africa 'there was a notable proliferation of hominoid primates, seven species in all; and there were at least five species of prosimians'. Primates became much less common in east Africa during the middle Miocene, although during the 14 to 18 m.y. transition period monkeys were 'common at Maboko', whereas 'there is little evidence for their presence in the Early Miocene environments' (Andrews & Van Couvering 1975: 93). The primates are thus one group which reflect the 'abrupt changes' referred to earlier, but in this instance the change is not manifested in the southern African record.

The apparent absence of primates in southern Africa during the earlier part of the Miocene is made even more remarkable by the fact that this group features in the 'Burdigalian' faunal interchange between east Africa and southern Eurasia. Thus, while a northward movement of primates from east Africa is documented, there is no record of a corresponding movement to the south.

To sum up, there is some evidence which suggests that early in the Miocene faunal interchange between east and southern Africa was inhibited and that at least some related taxa evolved independently of one another in the two regions. This indicates the existence of an environmental barrier between the two regions and it is most likely to have been comprised of the extensive river system of central Africa, together with the Rift Valley lakes (see Kortlandt 1972). Even in their present form the Congo and Zambezi river systems, especially in the region of the Congo/Zambezi divide, make up a broad and almost continuous area of channels and marshes between east and south-west Africa. Tectonic disturbances in central Africa during the mid-Tertiary may well have complicated the headwater drainage patterns of these rivers and so have created an even more effective barrier to limit the crossing of at least certain mammals.

Another possible barrier may have been that of an intervening arid and semi-arid region. A more extended form of the present Kalahari desert would have effectively separated east and south-west Africa from one another. This alternative is perhaps less likely since the present aridity of the south-western parts of Africa was apparently initiated only in the very late Tertiary (A. J. Tankard & J. Rogers, unpublished manuscript). Prior to this the climate and vegetation of Africa may have been of a more uniform nature.

The preceding observations suggest that in assessing the character and composition of southern African Miocene faunas, allowance must be made for deviations from the better documented east African pattern because geography is a complicating factor, the full implications of which have yet to be established.

In this connection the apparent absence of creodonts at Arrisdrift may also be significant. Creodonts predominate in the carnivore faunas of the 18 to 22 m.y. period in east Africa and the only identified carnivore from con-

temporary occurrences in the Namib is also a member of this group. Similarly the only recorded carnivore from Maboko is a creodont, while at Fort Ternan creodonts are common if not predominant. In other words, creodonts were an important element in the 'Aquitanian' to 'Vindobonian' faunas of east Africa. Consequently, it is to be expected that they would not only be present at Arrisdrift but would be more commonly represented than fissiped carnivores.

Since carnivores are less restricted by environmental factors than herbivores, the dispersal of immigrant taxa may well have been rapid in spite of barriers which impeded the movement of, for example, primates. Should it be established that creodonts are, indeed, rare or absent at Arrisdrift, the situation could be explained in only one of two ways.

Firstly, southern Africa was an important centre of fissiped evolution and they superseded creodonts in this region before the same happened in east Africa. This possibility can be dismissed in view of what is known of fissiped origins and evolution (Savage 1977) and since it would require complete isolation of southern Africa from east Africa during the early Miocene.

The second possibility is that Arrisdrift is younger than was indicated previously and dates from a period when the creodonts had been largely or completely replaced by fissipeds. The carnivores would then be the only obvious 'advanced' element in the Arrisdrift fauna, while those taxa which suggest a c. 16 m.y. date would be 'primitive' forms which survived longer in the Namib region than in east Africa. This interpretation would require, for example, that early bovids and giraffids such as those found at Fort Ternan had been prevented from spreading southwards by the hypothetical zoogeographic barrier, whereas immigrant fissipeds had already surmounted it and become established in southern Africa by the time that the Arrisdrift fossils were being deposited.

Perhaps the only firm conclusion to be drawn from the preceding discussion is that the present state of knowledge of southern African Miocene faunas leaves much to be desired.

Some information on the nature of the environment in the immediate vicinity of Arrisdrift at the time that the fossiliferous deposits were laid down is suggested by both the fossils and the deposits themselves.

There is no doubt that the fossils accumulated in a river channel, the vertebrate remains simply being an additional element in the coarse sediment fraction of a fluvial gravel. The fact that a *Prohyrax* skull and other delicate fossils were recovered from the deposits indicates that they at least could not have been transported far in what was evidently a turbulent channel. Even those specimens which are abraded are not seriously damaged. Thus, most of the fossils must represent the remains of animals which lived in the immediate vicinity or a little further upstream.

The only invertebrate in the fossil assemblage, a serpulid polychaete (cf. *Mercierella* sp.), is a typically estuarine form (B. Kensley, pers. comm.) and its presence suggests that at the time of deposition the coastline, which is at present

about 30 km away, was much closer. This, together with the fact that the fossiliferous deposits are about 50 m above sea-level, suggests that deposition took place during a period of relatively high sea-level. There is evidence for a world-wide marine transgression during the Miocene, between 10 and 20 m.y. ago (Flemming & Roberts 1973) and presumably at least part of the Arrisdrift terrace sequence can be correlated with this event. Arrisdrift is situated in a hilly area on the last meander of the Orange River before it reaches the flat and low-lying coastal section of its valley, which is likely to have been inundated during the transgression. The mouth of the river was, therefore, probably only a few kilometres west of Arrisdrift.

The area around Arrisdrift is now very arid, with Alexander Bay at the mouth of the Orange River having a mean annual rainfall of less than 50 mm (Dept. of Transport 1965). The Orange River is, however, a large perennial river and is flanked by a narrow belt of bushes and trees, although the vegetation becomes ephemeral a short distance away. There is little or no soil cover in the area and aeolian sands and bedrock exposures are ubiquitous. Although the climate is ameliorated by the proximity of the cold Atlantic Ocean, it is nevertheless an inhospitable area capable of supporting only sparse populations of a relatively small number of mammalian species (see Shortridge 1934).

The environment at the time that the fossils were deposited must have been very different. Although poorly preserved plant remains occur in the Pit 2/AD 8 deposits, no direct information on the nature of the vegetation is yet available. The large mammals, particularly the two proboscideans, suggest a densely vegetated and probably wooded environment. Harris (1975) has suggested that both *Prodeinotherium* and gomphotheres preferred such a habitat. The low-crowned teeth of the rhinoceros suggest that it, too, was a browser, while the long limbs and low-crowned teeth of the *Climacoceras* indicate that it was not adapted to grazing. Both are likely to have been woodland species.

The smaller herbivores are probably indicative of a dense undergrowth at least in the immediate vicinity of the river. Living tragulids are forest-dwelling browsers and their Miocene ancestors, including the Arrisdrift *Dorcatherium*, probably had a similar habitat preference. The same is likely to apply to the bovid and two suids since they resemble the *Dorcatherium* in both size and hypsodonty, while the *Prohyrax* probably occupied a similar habitat, but with somewhat different vegetable-food preferences.

Since later pliohyracines were aquatic or amphibious animals, early forms such as the Arrisdrift *Prohyrax* may already have developed a preference for life in water-side situations. The fact that it is the most commonly occurring vertebrate in the assemblage supports the theory that it was a riparian species since remains of such animals are more likely to be incorporated in fluvial deposits than those of other terrestrial species. In this connection it is probably significant that the other commonly occurring vertebrate at Arrisdrift is a crocodile, which undoubtedly is a riparian species.

The picture which emerges is of a forested riverine setting, probably with

dense undergrowth adjacent to the river and with the sea no more than a few kilometres away. An essentially similar environment was suggested for those areas further north in the Namib where the early Miocene vertebrates were discovered (Stromer 1926; Hopwood 1929). In the case of these occurrences the contrast to the modern environment is even more striking since there are no rivers in the area today. There is, however, ample evidence of their presence during the Miocene.

The Arrisdrift fossils, together with the older ones from the Lüderitz–Bogenfels area, provide some of the evidence which supports the theory that the present Namib desert is relatively young (A. J. Tankard & J. Rogers, unpublished manuscript). Whether or not a desert existed in the area in pre-Miocene times is still a matter of dispute, but the earlier part of the Miocene was evidently a period of relatively high rainfall and more luxuriant vegetation.

Andrews & Van Couvering (1975) believed that during this period a belt of lowland forest stretched across equatorial Africa and was flanked on either side by woodlands. The evidence from Arrisdrift and the other occurrences suggests that these woodlands extended at least as far south as the Orange River.

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